

Adaptive responses of *Acer ginnala*, *Pyrus ussuriensis* and *Prunus davidiana* seedlings to soil moisture stress

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Abstract: One-year-old seedlings of Amur maple (*Acer ginnala* Maxim), Ussurian pear (*Pyrus ussuriensis* Maxim) and David peach (*Prunus davidiana* Carr) were planted in pots in greenhouse and treated with four different soil moisture contents (75.0%, 61.1%, 46.4% and 35.4%). The results showed that net photosynthesis rate (NPR), transpiration rate (TR) and stomatal conductance (Sc) of seedlings of the three species decreased with the decrease of soil moisture content, and Amur maple seedlings had the greatest change in those physiological indices, followed by Ussurian pear, David peach. Amur maple and Ussurian pear seedlings also presented a decrease tendency in water use efficiency (WUE) under lower soil moisture content, whereas this was reversed for David peach. Under water stress the biomass allocation to seedling root had a significant increase for all the experimental species. As to root/shoot ratio, Amur maple seedlings had the biggest increase, while David peach had the smallest increase. The leaf plasticity of Amur maple seedlings was greater, the leaf size and total leaf area decreased significantly as the stress was intensified. No significant change of leaf size and total leaf area was found in seedlings of Ussurian pear and David peach. It was concluded that Amur maple was more tolerant to soil moisture stress in comparison with David peach and Ussurian pear.

Keywords: Moisture stress; Net photosynthesis rate; Water use efficiency; Biomass allocation; *Acer ginnala*; *Prunus davidiana*; *Pyrus ussuriensis*.

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Introduction

Green plants are very important component for urban ecosystem (Wang 1995; Zhu *et al.* 2001). Lack of tree species for northern cities has posed long lasting ecological problems in the northern cities: low biodiversity, lower stabilization (Zhang 2001), and the dull landscape, etc. The key solution to solve those problems depends upon quick introduction of tree species to urban area. Since bunch of environmental stresses retard the process of species introduction to urban area, the adaptability of species to the very stresses in urban environment should be given enough concern (Zhang 1999).

Soil moisture stress is one of the common stresses in urban environment in northeast China, which poses a great problem on the growing and development of tree species in cities. Under the stress, plants may take advantage of physiological and/or morphological responses to adapt themselves to the environmental stress. The adaptability of different plant species to moisture stress could be assessed from their morphological and physiological response (Peng 1998; Yang *et al.* 2002).

The primary response of plant to moisture stress is the

decrease of net photosynthetic rate (NPR) and stomatal conductance (Sc) (Ranney *et al.* 1990; Ni *et al.* 1991; Zhang *et al.* 1997; Arndt *et al.* 2001; Rieger *et al.* 2003). With the development of moisture stress, Sc decreases exponentially, and NPR decreases linearly (Zhang *et al.* 1997). The reason that NPR decreases under soil moisture stress was stomatal limitation at the first stage of stress development, whereas non-stomatal limitation dominated when the stress became more severe (Seppo *et al.* 1996). Water use efficiency (WUE), indicating the ratio of NPR to transpiration rate (TR), decreased at less severe stage, but increased at severe stress stage (Ranney *et al.* 1990; Arndt *et al.* 2001; Ni *et al.* 1991; Zhang *et al.* 1997).

Leaf morphological traits changed when the stress last long enough (Cregg *et al.* 1994). Decrease of single leaf area (Marc *et al.* 1994; Cregg *et al.* 1994; Osório *et al.* 1998) and specific leaf area (SLA) (Marc *et al.* 1994), and increase of leaf thickness and stoma density (Marc *et al.* 1994) have been reported.

The accumulation and distribution of biomass of individual plants changed correspondingly to the decrease of photosynthesis efficiency and leaf area, total biomass accumulation usually decreased (Osório *et al.* 1994; Zhang *et al.* 1997; Osório *et al.* 1998), and relative biomass allocated to root increased (Ranney *et al.* 1990; Cregg *et al.* 1994; Arndt *et al.* 2001).

The tolerance of tree species to moisture stress could be evaluated according to the response of above indices under moisture stress conditions (Yang *et al.* 2002; Wang *et al.* 2002).

Amur maple (*Acer ginnala* Maxim), Ussurian pear (*Pyrus*

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ussuriensis Maxim), and David peach (*Prunus davidiana* Carr) are common tree species native to the mountainous area of the Northeastern China. These tree species have some excellent traits, such as beautiful shape, distinguished seasonal appearance, etc., and are potentially valuable for ornamental purpose. However, less knowledge on the ecological traits of these tree species limits introduction of the species to urban areas.

The purpose of our work was to test the adaptability of these species to moisture stress from perspectives of tree physiology, morphology and biomass allocation. Some baseline data was expected to make available for the utilization of these tree species as ornamental plants.

Materials and methods

Materials

The experiment was conducted in greenhouse at Jilanlagou Research Forest Station, Northeast Forestry University. The one-year-old seedlings of Amur maple, David peach, and Ussurian pear were purchased from local nursery.

Experiment layout

The seedlings were transplanted to plastic pots (25 cm in height and 30 cm/23 cm in diameter at uppermost/bottom) in July 2001. The medium was dark-brown forest soil, a fertile zonal forest soil to Northeast China. Soil field moisture capacity was 33.3%. Four seedlings were grown in each pot. The seedlings were properly watered for the first four weeks for the establishment, then divided into 4 groups, 5 pots each group as replications. Four watering regime were conducted to produce soil moisture gradient. Soil relative moisture contents were: A: 75.0%; B: 61.1%; C: 46.4%; D: 35.4%, respectively, for the four treatment. The soil moisture was sustained by qualified watering (weighing the pots) at 5:00 p.m. every day. The treatment lasted 45 days, then made the measurement and seedlings harvest.

Data collection

The measurement was conducted in sunny days in August. Leaves from relatively same position on the seedlings, with approximately same size and maturity, were selected for determining the NPR, TR, Sc, intercellular CO₂ concentration (Ci). Leaf WUE was calculated with formula $WUE = NPR/Tr$ (Shangguan 1999). Three leaves of seedlings from each treatment were measured, and the measurement was repeated for 5 times for each leaf. The environmental features were recorded as follows: atmosphere CO₂ concentration, $367.1 \pm 7.4 \mu\text{mol} \cdot \text{mol}^{-1}$; photosynthesis available radiation (PAR), $1567.0 \pm 83.8 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$; air temperature, $26.3 \pm 2.1^\circ\text{C}$; leaf surface air temperature, $30.5 \pm 2.9^\circ\text{C}$.

Five mature leaves from each treatment were chosen from east, south, west and north aspects, respectively, and the leaf length and width was measured with calipers, which were used to indicate individual leaf size (Pu *et al.*

2000). Total leaf area of a seedling was calculated followed the method of leaf mass weighting (Wang 1991). The root, stem and leaves were oven dried at 75°C to constant weight, and weighted. The ratios of root, stem and leaf dry mass to total biomass were determined. Root was divided into fine root (<2mm) and coarse root (>2mm), and the ratios of fine root and coarse root to total root weight were calculated. The specific leaf area (the ratio of leaf area to leaf dry mass) was also determined.

Results and analysis

Gas exchange and WUE of seedlings under different soil moisture treatments

The NPR and TR of seedlings of all the tree species decreased at lower soil moisture content (Table 1). Comparing with seedlings treated with 75% soil moisture content (Treatment A), the NPRs of Amur maple, Ussurian pear, David peach seedlings under treatment of 35.4% soil moisture content (Treatment D) decreased relatively by 79.0%, 71.7%, and 17.4%, respectively; and the TR decreased by 63.0%, 32.2% and 19.0%, respectively.

Under moisture stress treatment, the stomatal conductance (Sc) of the seedlings also decreased (Table 1). The relative decrease of Sc of the seedlings under treatment of 35.4% soil moisture content were Amur maple (79.2%)> Ussurian pear (73.6%)> David peach (55.6%) in relation to that under treatment of 75% soil moisture content.

The Ci of different tree species followed different trends, with that of David peach decreased under soil moisture stress treatment, and that of Amur maple and Ussurian pear decreased at first stage, but increased at more intensified moisture stress (Table 1).

Significant difference among the WUE of tree species was also detected. The WUE of Amur maple and Ussurian pear seedlings decreased at lower soil moisture content, the relative decrease of WUE of Amur maple and Ussurian pear seedlings under treatment D is 57.0% and 34.8% in relation to that under treatment A, respectively. In contrast, the WUE of David peach seedlings increased by 21.6% at D treatment in relation to A treatment (Table 1).

Leaf dimension of seedlings under different soil moisture treatments

The plasticity of individual leaf to soil moisture was different between the species tested. The leaf length and width of Amur maple were more sensitive to the change of soil moisture in comparison to that of other two tested species. Significant decrease was found with the leaf dimension of Amur maple at low soil moisture content. Compared with A treatment, the leaf length and leaf width of Amur maple under treatment D decreased by 14.9% and 11.1%, respectively. No significant differences between treatments were found with Ussurian pear and David peach seedlings (Table 2).

The specific leaf area (SLA) and total plant leaf area

(TPLA) of Amur maple had a decrease trend with the decreasing of soil moisture. No significant differences in SLA and TPLA were found between treatments of different soil moisture stresses for Ussurian pear and David peach seedlings (Table 2).

Biomass allocation of seedlings under different soil moisture treatments

No significant intraspecific differences in total biomass of seedlings under different soil moisture treatments were produced. The relative allocation of biomass varied significantly with species under different soil moisture treatments

(Table 3). With the decrease of soil moisture, the ratio of root biomass to total biomass, root biomass to shoot biomass, and fine root biomass to total root biomass of the seedlings of all the species significantly increased.

In comparison to those under treatment A (75.0% relative soil moisture content), the ratio of root biomass to total biomass, ratio of root biomass to shoot biomass, and the ratio of fine root biomass to total root biomass of seedlings under treatment D (35.4% relative soil moisture content) relatively increased by 61.3%, 117.4%, and 38.2% for Amur maple, 34.9%, 74.4%, and 26.3% for Ussurian pear, and 26.1%, 54.3% and 14.3% for David peach, respectively.

Table 1. Parameters of CO₂/H₂O gas exchange and WUE of seedlings under different soil moisture treatments

Species	Treatment Soil moisture content %	NPR / $\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$	TR / $\text{mmol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$	Ci / $\mu\text{l} \cdot \text{l}^{-1}$	Sc / $\text{mmol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$	WUE / $\mu\text{mol} \cdot \text{mmol}^{-1}$
<i>Acer ginnala</i>	A: 75.0%	10.76(2.66) ^a	3.19(1.07) ^a	238.00(19.85) ^a	142.60(21.51) ^a	3.37(0.28) ^a
	B: 61.1%	7.61(1.58) ^b	2.89(0.53) ^{ab}	211.65(17.19) ^{ab}	103.90(10.76) ^b	2.63(0.22) ^b
	C: 46.4%	6.51(1.53) ^b	2.70(0.32) ^b	203.47(19.85) ^b	84.05(6.22) ^c	2.41(0.26) ^b
	D: 35.4%	2.26(1.32) ^c	1.18(0.54) ^c	241.85(17.19) ^a	29.68(6.97) ^d	1.92(0.31) ^c
	P-value	0.038*	0.033*	0.032*	0.0017**	0.032*
<i>Pyrus ussuriensis</i>	A: 75.0%	15.46(1.53) ^a	5.67(1.75) ^a	296.23(16.15) ^a	438.73(100.39) ^a	2.73(0.11) ^a
	B: 61.1%	13.84(2.66) ^b	5.87(1.39) ^a	271.50(25.33) ^{ab}	349.28(12.24) ^b	2.36(0.19) ^a
	C: 46.4%	10.18(2.45) ^b	5.23(0.91) ^a	262.10(6.15) ^b	243.57(16.05) ^c	1.95(0.17) ^b
	D: 35.4%	4.38(1.42) ^c	4.59(1.33) ^b	308.20(27.54) ^a	115.90(10.30) ^d	0.95(0.22) ^c
	P-value	0.029*	0.044*	0.037*	0.0013**	0.0029**
<i>Prunus davidiana</i>	A: 75.0%	8.24(1.85) ^a	4.69(1.05) ^a	301.85(18.58) ^a	225.88(21.90) ^a	1.76(0.21) ^a
	B: 61.1%	9.13(1.98) ^a	4.79(0.97) ^a	292.50(9.91) ^a	198.87(23.34) ^b	1.91(0.24) ^a
	C: 46.4%	9.84(2.28) ^a	4.75(1.37) ^a	293.00(10.91) ^a	165.70(13.34) ^c	2.07(0.24) ^b
	D: 35.4%	6.81(1.15) ^b	3.18(0.86) ^b	254.75(28.58) ^b	100.28(12.90) ^d	2.14(0.21) ^b
	P-value	0.036*	0.056*	0.014*	0.023*	0.039*

Note: Data in parenthesis represent standard error; P-value: *, **: significantly different at $p < 0.05$, $p < 0.01$ level; Data with different letters are significantly different at $p > 0.05$ level, by LSD post hoc comparison. Same within the following tables.

Table 2. Leaf characters of seedlings under different soil moisture treatments

Species	Treatment Soil moisture content %	Total plant leaf area / cm^2	Specific leaf area / $\text{cm}^2 \cdot \text{g}^{-1}$	Leaf length / cm	Leaf width / cm
<i>Acer ginnala</i>	A: 75.0%	343.6 (36.0) ^{ab}	250.5(5.4) ^a	6.7(1.1) ^a	5.4(0.1) ^a
	B: 61.1%	408.1(51.0) ^a	211.7(4.1) ^b	7.0(0.8) ^a	5.9(0.1) ^a
	C: 46.4%	264.8(19.0) ^{bc}	209.3(6.4) ^b	5.9(0.7) ^b	4.9(0.1) ^b
	D: 35.4%	233.8(17.9) ^c	219.2(5.7) ^b	5.7(0.6) ^b	4.8(0.1) ^b
	P-value	7.2E-4**	4.5E-4**	9.0E-14**	3.4E-13**
<i>Pyrus ussuriensis</i>	A: 75.0%	313.2(53.9)	160.0(6.5)	8.5(1.4)	5.7(0.1)
	B: 61.1%	343.2(39.6)	165.5(6.7)	8.2(0.8)	5.4(0.2)
	C: 46.4%	303.7(44.0)	159.8(4.4)	7.6(1.4)	5.4(0.1)
	D: 35.4%	311.7(54.3)	176.6(9.3)	8.0(1.9)	5.3(0.1)
	P-value	0.36	0.30	0.18	0.21
<i>Prunus davidiana</i>	A: 75.0%	483.6(74.9)	259.7(10.7)	10.8(1.1)	4.5(0.1)
	B: 61.1%	481.0(132.7)	266.3(8.7)	10.4(1.4)	4.7(0.1)
	C: 46.4%	407.0(83.2)	271.6(16.3)	11.0(1.6)	4.6(0.2)
	D: 35.4%	408.8(55.3)	246.2(8.9)	10.4(1.7)	4.3(0.1)
	P-value	0.26	0.45	0.32	0.28

Discussion

The NPR, Sc, and Ci in David peach seedlings de-

creased with the decrease of soil moisture (Table 1), which indicated that stomatal limitation was the primary factor affecting NPR by decrease the stomatal aperture (Berry *et al.* 1982). The NPR and Ci of Amur Maple and Ussurian

pear seedlings decreased under moderate soil moisture stress but increased as the stress level increased (Table 1), indicating that the stomatal limitation was the primary factor affecting NPR, and then nonstomatal limitation became more important, the decrease of photosynthetic activity of mesophyll cells was believed to be the main cause (Daniel *et al.* 1993; Xu 1997).

The Sc and TR in the seedlings of the three tree species decreased with the decrease of soil moisture. The highest variation of Sc and TR was detected in Amur maple seedlings among different treatments, indicated that the stomata of Amur maple was more sensitive to moisture stress and

the stomata transpiration was the primary transpiration approach. Comparing the Sc and TR of Ussurian pear seedlings under 35.4% soil moisture (treatment D) to that under 75.0% soil moisture (treatment A) (73.6% and 19.0%, respectively), the relatively lower variation of Sc change indicated that there was, most probably, other transpiration approach for this species, such as cuticle transpiration (Ni *et al.* 1991). In relation to TR, the variation of NPR of Ussurian pear was greater (71.7%), indicated that the photosynthesis of Ussurian pear was more sensitive to moisture stress than transpiration.

Table 3. Biomass allocation of seedlings under different soil moisture treatments

Species	Treatment	Total biomass (g)	Root/total biomass	Root-shoot ratio	Fine root/total root biomass
<i>Acer ginnala</i>	A: 75.0%	3.08(0.46)	0.31(0.01) ^a	0.46(0.03) ^a	0.56(0.02) ^a
	B: 61.1%	4.28(1.18)	0.42(0.02) ^b	0.73(0.07) ^b	0.51(0.02) ^a
	C: 46.4%	3.46(0.4)	0.43(0.02) ^b	0.78(0.06) ^b	0.57(0.01) ^a
	D: 35.4%	3.54(0.4)	0.50(0.02) ^c	1.00(0.05) ^c	0.64(0.03) ^b
	P-value	0.094	6.6E-7**	5.56E-7**	3.3E-3**
<i>Pyrus ussuriensis</i>	A: 75.0%	5.68(0.99)	0.43(0.03) ^a	0.82(0.11) ^a	0.34(0.02) ^a
	B: 61.1%	5.10(0.78)	0.49(0.02) ^b	1.01(0.09) ^b	0.34(0.03) ^a
	C: 46.4%	5.75(1.56)	0.57(0.01) ^c	1.32(0.05) ^c	0.38(0.02) ^{ab}
	D: 35.4%	5.44(1.51)	0.58(0.02) ^c	1.43(0.13) ^c	0.47(0.03) ^b
	P-value	0.25	2.2E-5**	4.4E-4**	4.2E-4**
<i>Prunus davidiana</i>	A: 75.0%	5.08(1.16)	0.46(0.03) ^a	0.92(0.09) ^a	0.57(0.02) ^a
	B: 61.1%	6.59(1.86)	0.50(0.01) ^{ab}	1.01(0.05) ^{ab}	0.64(0.02) ^b
	C: 46.4%	5.35(1.35)	0.56(0.02) ^{bc}	1.31(0.09) ^{bc}	0.69(0.02) ^{bc}
	D: 35.4%	5.76(1.1)	0.58(0.02) ^c	1.42(0.08) ^c	0.72(0.02) ^c
	P-value	0.786	2.6E-4**	1.3E-4**	1.5E-5**

It has been well documented that Sc, TR, and NPR usually decrease as the moisture stress level increase within certain range of moisture stress, while the WUE increases (Ranney *et al.* 1990; Arndt *et al.* 2001; Sun *et al.* 1999; He *et al.* 2000; Wang *et al.* 2002). Increasing WUE is one of the main mechanisms that plants adapt themselves to moisture stress (Cowan 1982). In our experiment, with the decrease of soil moisture, the decrease amount of NPR (17.4%) of David peach was less than that of TR (32.2%), hence the higher WUE, indicating certain degree of adaptability of David peach to drought.

The variation of leaf length and width showed that Amur Maple was more sensitive in term of leaf size to moisture change than the other species. The single leaf area, TPLA, and SLA of Amur maple decreased as the stress level increased, while same variations were not found in Ussurian pear and David peach seedlings. It has been shown in the previous studies that under moisture stress, single leaf area (Marc *et al.* 1994; Cregg *et al.* 1994; Osório *et al.* 1998; Sun *et al.* 2000; Wang *et al.* 2001; Wang *et al.* 2002), TPLA (Osório *et al.* 1994; Rieger *et al.* 2003), and SLA (Marc *et al.* 1994; Wang *et al.* 1998; Sun *et al.* 1999) decreased under water stress. These changes enabled plants to control water loss through leaf surface (Arndt *et al.* 2001), which im-

proved the drought tolerant ability of plants (Larcher 1980). The significant change of these indices of Amur maple indicated that tolerance of this species to moisture stress was greater than that of the other two species tested in this very aspect.

The three tree species have the same biomass allocation pattern under moisture stress. Under severe moisture stress, relatively more biomass allocated to underground part, hence the higher root to shoot ratio (Table 3), which would improve the ability of plants to gain more water from soil and maintain water balance (Ranney *et al.* 1990). The relative shift of root to shoot ratio under treatment D vs treatment A varied greatly for the species tested, Amur maple (117.4%)>Ussurian pear (74.4%)>David peach (54.3%), indicated that Amur maple was more flexible to soil water stress in term of biomass allocation.

It has been demonstrated that plant biomass usually decrease under moisture stress (Osório *et al.* 1994; Zhang *et al.* 1997; Osório *et al.* 1998; Sun *et al.* 2000; Wang *et al.* 2001), nevertheless, in our study, no significant difference of total biomass produced among different treatments. Same result was achieved by Khalil *et al.* (1992) when they were testing the response of the *Acer ginnala* to moisture stress. Wang *et al.* (2001) also obtained the same result

with *Quercus mongolia* seedlings. They attributed this phenomenon to the stronger drought resistance of the species studied. In our case, same speculation could not be made; longer span for treatment might produce different result with different species.

According to the analysis of physiological and morphological indices, and biomass allocation pattern under moisture stress conditions, we concluded that all species tested could adapt themselves to moisture stress, but in different ways, and differed in the extent. Integrating all the variation of indices under moisture stress, we believe that *Acer ginnala* is more adaptive tree species to moisture stress in comparison to *Prunus davidiana* and *Pyrus ussuriensis*.

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